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A REMARKABLE LIFE HISTORY AND ITS MEANING.[1]

BY W. K. BROOKS.

NAVIGATORS in tropical seas often speak of sailing for days through regions where the water of the ocean, to a depth of many feet, is filled with small transparent animals, which are attached to each other in such a way as to form chains or trains like trains of cars. Although these animals are perfectly transparent and jelly-like in appearance, the fact that their bodies are of sufficient consistency to admit of their being somewhat roughly handled, or even removed from the water, without essentially changing their shape, at once distinguishes them from such animals as jelly-fishes; and a very superficial examination is enough to show that they are quite different from these in organization. They belong to the group Tunicata, animals which have been classed with the Mollusca, although we now know that the resemblances which formerly led naturalists to this idea of their affinity are merely superficial, and without scientific value.

Most of the Tunicata are, in their adult state, attached to heavy bodies which rest upon the bottom of the ocean; stones and shells, for instance. A few, however, are locomotive and are to be met with swimming at the surface; most of the latter belong to the genus *Salpa*, and to these we will at present confine our attention. Although the Salpæ are most often met with in the warmer parts of the ocean, they are by no means confined to the tropics, but have been found south of the most southern point of Australia, and north of Scotland and Norway. They are abundant only after the water has been for some time undisturbed by winds, and as calms are more frequent within the

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[1] A paper read before the Kirtland Society of Natural History of Cleveland, Ohio. The cuts are from a paper upon the development of Salpa, in the Bulletin of the Museum of Comparative Zoölogy, and were kindly loaned for this article by Mr. Agassiz.

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tropics than in more northerly or southerly latitudes, the former seas are more favorable than the latter to the development of these animals, which multiply with astonishing rapidity when furnished with abundant food. As they feed upon the microscopic

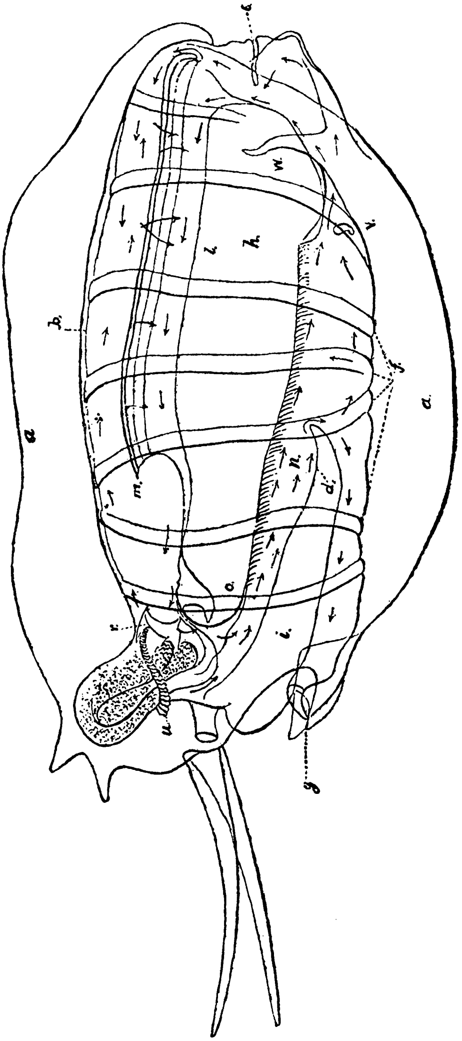


FIG. 43. Side view of an adult solitary Salpa, with the hæmal surface above: *a*, test; *b*, outer tunic; *d*, wall of atrial chamber; *e*, branchial aperture; *f*, muscular girdles; *g*, atrial aperture; *h*, breathing chamber; *i*, atrial chamber; *l*, epipharyngeal fold; *m*, endostyle; *n*, gill; *o*, mouth; *r*, heart; *u*, chain of males; *v*, ganglion; *w*, languette.

rhizopods which swarm at the surface of the ocean after a long-continued calm, they are then met with in numbers which defy description, and cannot be conceived by those who have not actually seen them.

Although single animals of our species are from one half to two thirds of an inch long, they are often so abundant that a bucket of water dipped at random from the surface of some sheltered bay will be found to contain many hundreds or even thousands. At such times collecting with the surface net becomes impracticable; for almost as soon as the net is placed in the water it becomes choked with a solid mass of Salpæ, so that nothing more can enter it, and unless Salpæ are what are wanted work must be abandoned until fresh winds again clear the water. A drop from an organic infusion swarming with Paramecia, seen under a low power of the microscope will give some conception of the appearance of the ocean when Salpæ are abundant, except that the water is not turbid like that of an infusion, but is perfectly fresh and clear; and no one who has not seen these animals under favorable conditions can form any conception of the amount of animal life which pure sea-water is able to support. The various species of Salpa vary in size, from those less than half an inch to those which are nearly a foot long, our species, as already stated, being about two thirds of an inch in length.

The animal (Figures 43 and 44) may be roughly described as a barrel or hollow cylinder, *b*, with a valvular opening at each end. The valves which guard the anterior opening (Figures 43, 45, and 55, *e*) are so arranged that while they allow the water to pass between them into the hollow chamber, *h*, they prevent it from passing out through the same opening; while those at the posterior opening (Figures 43, and 45, *g*) permit it to pass out but prevent its entrance. Around the barrel are a number of muscular belts like the hoops around a barrel (Figures 43, and 44, *f*), the contraction of which diminishes the capacity of the hollow chamber, *h*, and thus drives the water out through the posterior opening in a violent stream, which propels the animal forward. Upon the relaxation of these muscles a new supply of water passes in through the anterior opening, to be expelled in turn by the next contraction. As this pumping action is constantly going on, the animal is continually moving forward in a nearly straight line.

Wherever Salpa is found, two forms are met with, agreeing pretty closely in size and organization, but differing in outline and in some other slight details. (Compare Figures 43 and 45.) One of these forms, that shown in Figures 43 and 44, is called the "solitary Salpa," since each animal is entirely independent of all the others; while those of the other form (Figure 45) are called "chain-salpæ," since they are usually found united in a chain. Twenty-five or more of the barrel-shaped bodies are placed in a row, end to end, and each one is fastened to its neighbors before and behind it; this row is placed beside another similar to it, and each animal is fastened to two of its neighbors in the other row, so that the whole group of fifty or more forms a chain something like two trains of cars side by side on parallel tracks; only, to make the comparison more perfect, we must imagine each car chained to two cars in the other train, as well as coupled to those before and behind it. Since the animals are fastened in such a way that the posterior openings of all point in the same direction, all the streams of discharged water are driven in the same way and the whole chain moves forward with a uniform, steady motion. Figure 47 shows a few of the Salpæ from a chain, at a very early period of development, but as the animals are, unfortunately, not sufficiently far advanced at this time, the figure fails to give a very clear idea of the way in which they are united.

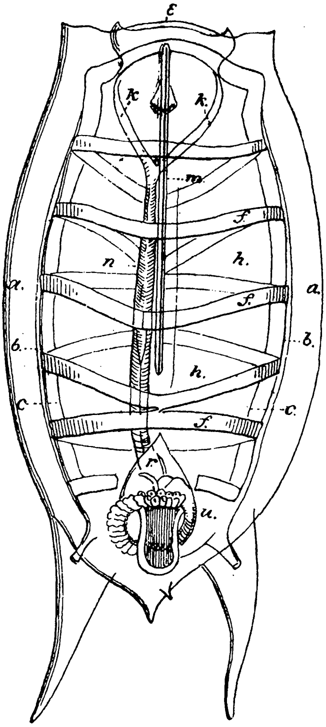


Fig. 44. Adult solitary Salpa, hæmal view : *a*, test ; *b*, outer tunic ; *c*, wall of breathing chamber ; *e*, branchial aperture ; *f*, muscular girdles; *h*, breathing chamber; *k*, peripharyngeal ridges; *m*, endostyle ; *n*, gill ; *nu*, "nucleus" or digestive organs ; *r*, heart; *u*, chain of males.

Salpa is very remarkable for the number of examples it presents of deviation from laws which are almost uniformly conformed to throughout the animal kingdom. One of the most striking of these anomalies is the periodical reversal of the action of the heart. This was discovered in 1824 by Van Hasselt, and although it is not peculiar to Salpa, but is shared by all the Tuni-

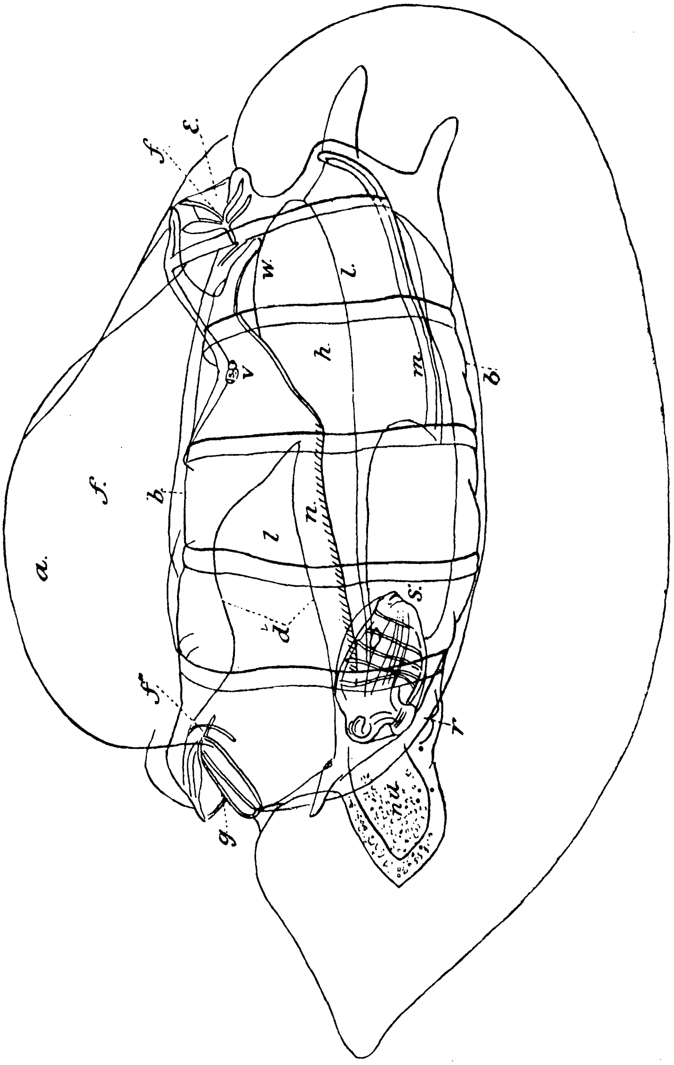


FIG. 45. Side view of adult chain-salpa, figured with the neural side uppermost: *a*, test; *b*, outer tunic; *d*, atrial tunic; *e*, branchial aperture; *f'*, muscles of branchial aperture; *f''*, muscles of atrial aperture; *g*, atrial aperture; *h*, breathing chamber; *l*, epipharyngeal fold; *m*, endostyle; *n*, gill; *r*, heart; *s*, embryo; *u*, ganglion; *w*, languette.

cata, can be best studied in this genus, owing to its transparency. The body of the animal is so perfectly transparent that the pulsations of the heart may be seen without difficulty, and with a microscope the circulation of the blood may be traced to all parts of the body. After beating regularly for some time the heart suddenly stops, and for an instant the blood of the whole body comes to rest; this stoppage does not last for more than a second, and the pulsation and circulation then recommence as vigorously as before, but in the opposite direction, so that the blood-channels which before served as arteries and carried blood from the heart now perform the function of veins.

More careful examination will show what is possibly the reason of these changes. The blood does not circulate in true vessels with distinct walls, but in the spaces between the various organs of the body; thus it often happens that a space or sinus may have a large passage leading to it on one side and a very small one on the other, and the blood which enters the chamber through the large passage, being unable to escape with equal rapidity through the small one, soon accumulates and forms a dam or obstruction. As soon as the current is reversed, this obstruction is, of course, driven away from the small opening and gradually discharged again through the large one. Another peculiarity which Salpa shares with the other tunicates is the presence of an outer shell or test containing "cellulose." Cellulose is the substance which forms most of the tissues of plants; and although it is almost universally present in vegetables, it is found in only a very few animals, and is often stated to be one of the features which distinguish the vegetable from the animal kingdom. Salpa, however, together with a few other animals, is partially composed of true cellulose. In Figures 43, 44, and 45 the cellulose test, *a*, is shown as a thick transparent shell or outer tube, covering the remaining organs of the body.

By far the most interesting peculiarity of our animals is that the two forms, which are always found in the same locality, are of the same species. Nearly fifty years ago Chamisso ascertained that the solitary Salpa gives birth to a chain, and that each of the chain-salpæ in turn gives birth to a single solitary Salpa; and to this phenomenon he gave the name of "alternation of generations." At about the same time he published his famous story of Peter Schlemihl, who, for an inexhaustible purse, sold his shadow to the devil, and, through lack of this important appendage to his body, became involved in numerous entertaining misfortunes and vexations which his money was powerless to prevent. At this time nothing was known in regard to the wonderful changes which so many of the invertebrates undergo in passing from the egg to the perfect form; and the existence of animals whose children resemble their grandparents, while they are quite unlike their parents, was so opposed to all that was known that Chamisso's discovery at first met with nearly universal ridicule and discredit. In fact, one of the greatest of naturalists is stated to have said that he could much more easily credit Chamisso's romance of Peter Schlemihl than his observations upon Salpa.

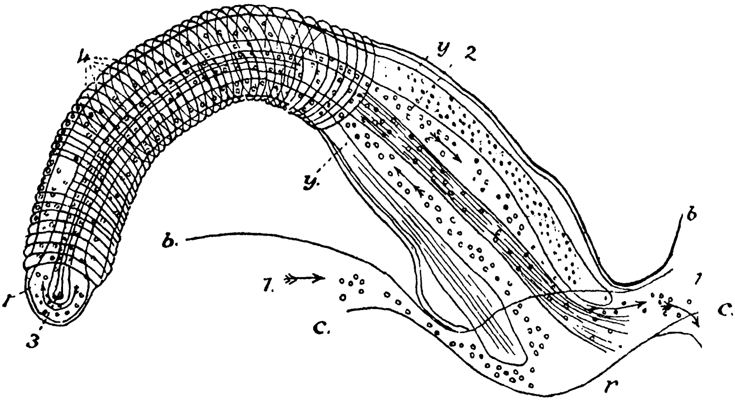


FIG. 46. Very young bud-tube, from a solitary Salpa: *b*, outer tunic; *c*, wall of pericardium; *r*, heart; 1, blood-channel; 2, cavity of tube; 4, constrictions upon the tube; *yy*, ovaries.

At this time our acquaintance with the lower invertebrates was increasing with wonderful rapidity, and it was soon found that several animals, especially the intestinal worms, go through an alternation substantially like that described by Chamisso as taking place in Salpa; the second generation being very different in external form, and, in many cases, in structure also, from the first. Within a few years from the time of publication of Chamisso's account Steenstrup's work upon Alternation of Generations appeared, and so much additional information was given by this that this method of development was shown to be not even anomalous or exceptional, but common to whole groups of animals. Salpa also was soon made an object of especial study by several eminent naturalists, and Chamisso's account was confirmed in all essential particulars; and the able memoirs of Sars, Krohn, Huxley, Vogt, and Leuckart have given us a nearly complete account of its life history. All these naturalists agree in holding the opinion that Salpa presents a real alternation of generations, as stated by Chamisso, and the history of its development, as given in their papers, is as follows: —

Each egg hatches into a single embryo of the solitary form (Figures 43 and 44). After this solitary Salpa has acquired most of the adult characteristics, but while it is still very small, part of the wall of its body becomes prolonged into a hollow tube, which is shown, very much magnified, in Figure 46. The cavity of this tube is in free communication with one of the blood-channels (1) of the mother, so that the blood can pass into and out of the tube and thus supply the material for its growth and development. The tube lengthens very rapidly, and as it grows it bends so as to pass round the digestive organs of the mother (Figure 44, *nu*) in a spiral (*u*) which lies between these organs and the outer wall of cellulose. Meanwhile a series of constrictions makes its appearance upon the surface of the tube (Figure 46), and in a short time the spaces marked off by these constrictions assume the shape and acquire the organs of young chain-salpæ, as shown in Figure 44, *u*. The chain-salpæ then are produced by a process of budding from the body of the solitary Salpa.

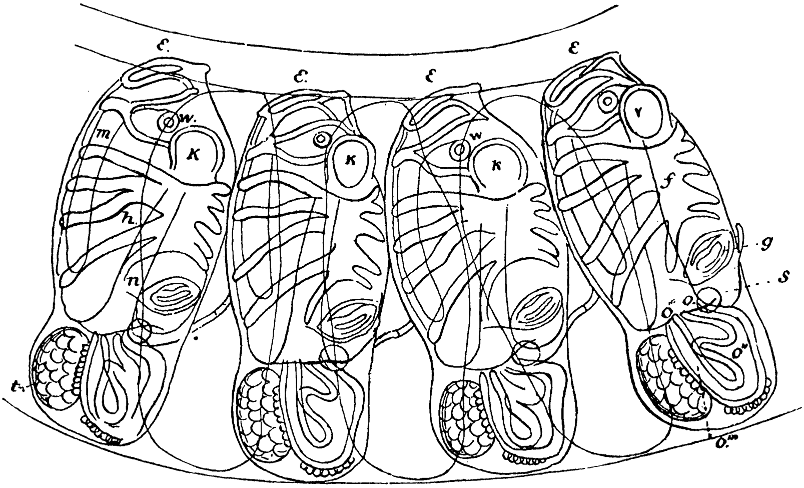
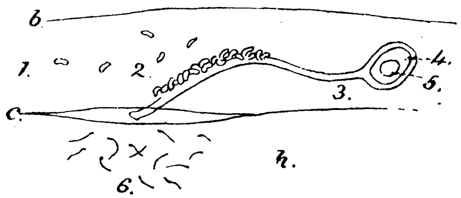
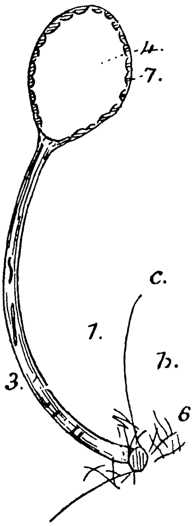


Fig. 47. Seven animals from a fully developed chain immediately before its discharge from the body of the solitary Salpa: *s*, egg; *t*, testicle.

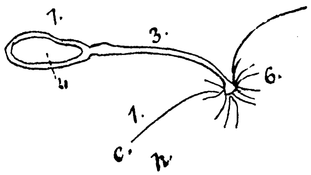
There are many hundred chain-salpæ thus marked off at one time upon the surface of the tube, but the forty or fifty nearest its free end develop much more rapidly than the rest, though uniformly as compared with each other. After their organs are perfectly formed, but while they are still very small, they become detached from the tube and escape into the water as a chain, the animals of which are now able to provide for themselves and grow very rapidly. Meanwhile another set is developed upon the tube of the solitary form, to be cast off in turn, so that the



(FIG. 48.)

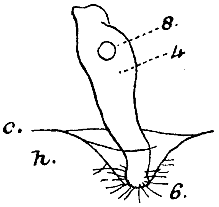


(FIG. 49.)

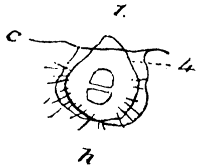


(FIG. 50.)

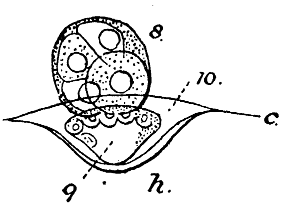
FIG. 48. Egg before impregnation.
FIG. 49. Egg during impregnation.
FIG. 50. The changes following impregnation : *b*, outer tunic of nurse ; *c*, wall of breathing chamber of nurse ; *h*, breathing cavity of nurse ; 1,blood-channel of nurse ; 2, blood corpuscles ; 3, egg-stem ; 4, yolk ; 5, germinative vesicle ; 6, spermatozoa ; 7, capsule of egg ; 8, nucleus.



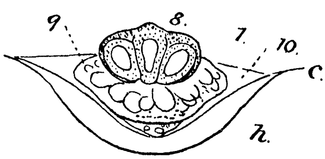
(FIG. 51.)



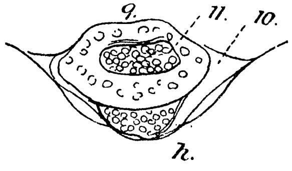
(FIG. 52.)



(FIG. 53.)



(FIG. 54.)



(FIG. 55.)

FIGS. 51–55. Successive stages of segmentation : *c*, wall of breathing chamber of nurse ; cavity of same ; 1, blood channel ; 4, yolk ; 8, food yolk ; 9, germ yolk; 10, orifice of blood sac ; 11, invagination orifice ; *h*, breathing cavity of nurse.

latter continues to set free chains from time to time, as they become matured.

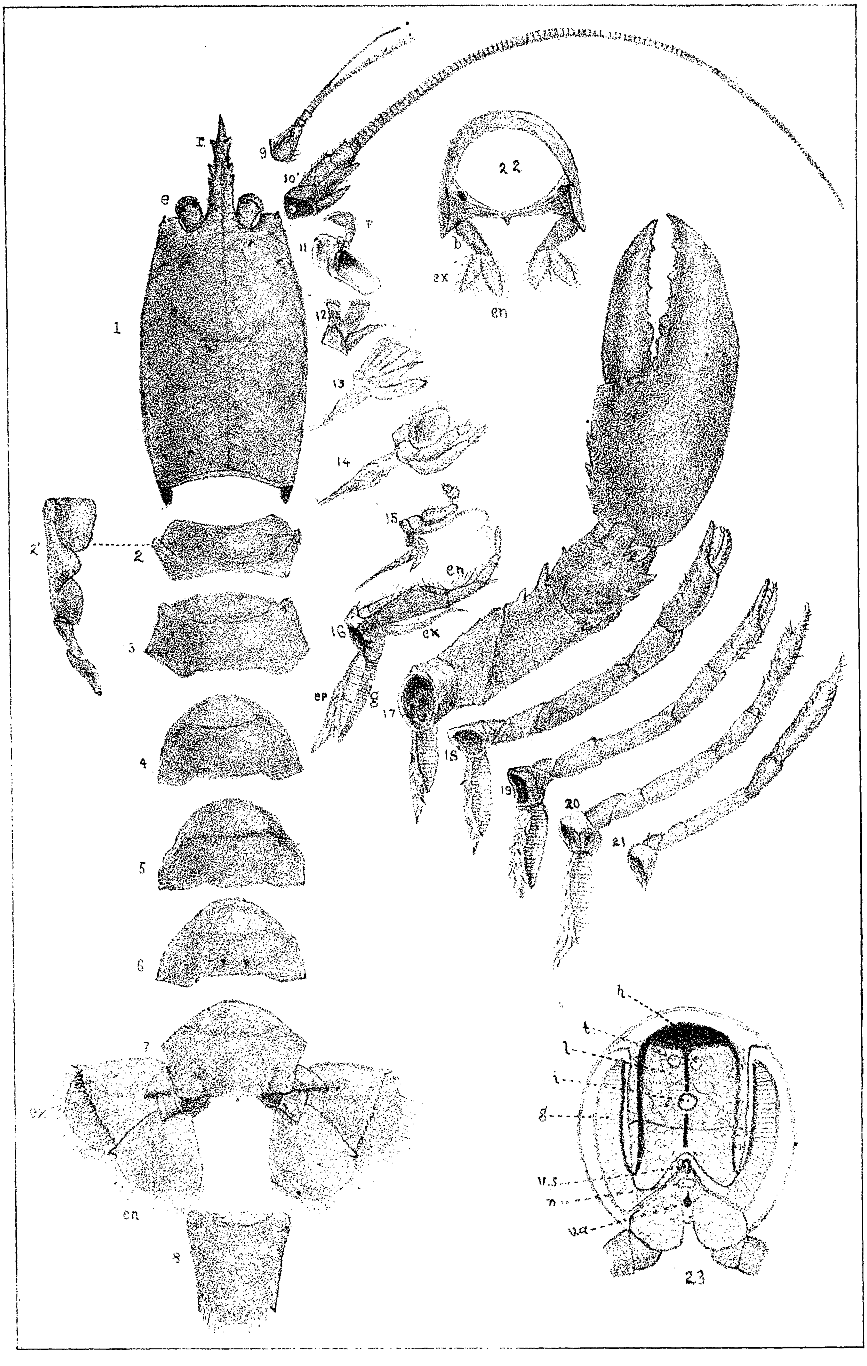
The solitary Salpas themselves are produced in quite a different way. At the time the chain is set free each of its component animals contains a single egg (Figure 47, *s*) as well as a testicle (*t*), which is at this time immature and is composed of a mass of undifferentiated cells, as shown in the figure.

The eggs, on the contrary, are fully developed and ready for impregnation, which soon takes place, and is accomplished in a very remarkable manner. The egg (Figure 48) lies in one of the blood-channels (1) of the chain-salpa, which we shall hereafter call the " nurse." It is bathed freely by the blood, but is not itself free within the channel, being mounted upon a long stalk (3), like a cherry upon its stem, and the end of this stem is attached to the large chamber (Figure 45, *h*), which we have already described as filled with sea-water, and which we shall hereafter designate as the breathing chamber.

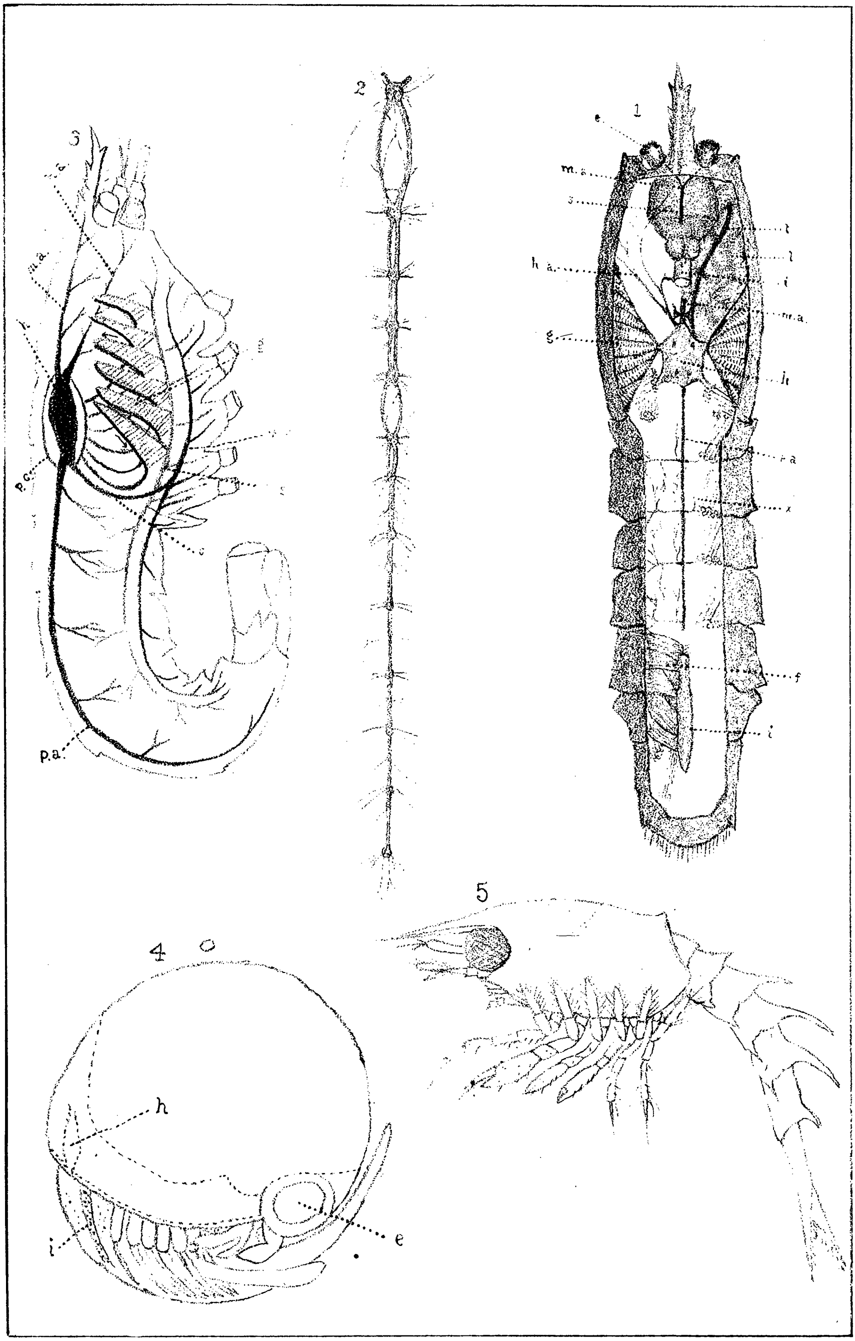
In Figure 48, *c* represents the wall of this breathing chamber, and *h* its cavity, which is open externally and is filled with water at each contraction of the muscular bands. As Salpa when found at all is very abundant, the water always contains plenty of full-grown chains, as well as the young and immature egg-bearing ones. The testicle in the full-grown chain-salpa is fully formed, and this discharges its spermatic fluid into the water, which accordingly contains great numbers of fresh and actively moving spermatozoa. Some of these are drawn, with the respired water, into the breathing chambers of the young nurses, and these may be seen to congregate at the point where the egg-stem is attached, as shown in Figures 48, 49, and 50. Some of these may be seen to penetrate the stem, and work their way up towards the egg, which is thus fertilized. After impregnation the stem shortens and swells as shown in Figures 49, 50, and 51, and draws the egg down into a "brood-chamber," or pouch, which is formed in the wall of the breathing chamber. The opening of this pouch still connects it with the blood-channel, of which its cavity is a diverticulum, so that the egg is still bathed and nourished on all sides by the blood, and increases in size very rapidly during segmentation, some of the stages of which process are shown in Figures 51, 52, 53, and 54. After the formation of the gastrula the blood not only bathes the outside of the embryo but also passes into and out of the gastrula mouth (Figure 55, 11).

A constriction now makes its appearance and divides the em-

PLATE V.



Anatomy of the Lobster.



Anatomy and Development of the Lobster

bryo into two portions, of which the one nearest the blood channel of the nurse becomes developed into a true placenta (Figure 56, 12), similar, in function as well as in structure, to that of a

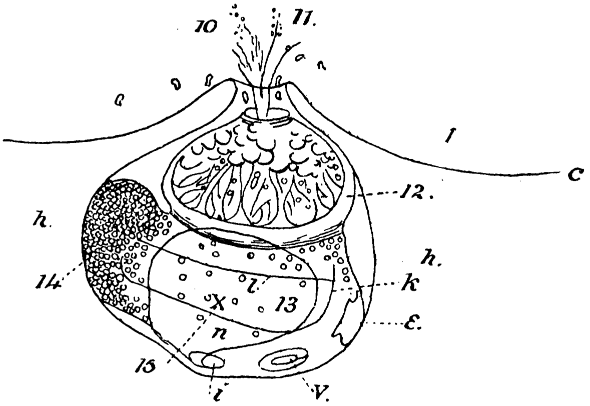


FIG. 56. Embryo of solitary Salpa.

fœtal mammal, while that portion which is directed towards the breathing chamber becomes developed into the embryo proper. This is nourished with the blood of the nurse by means of the

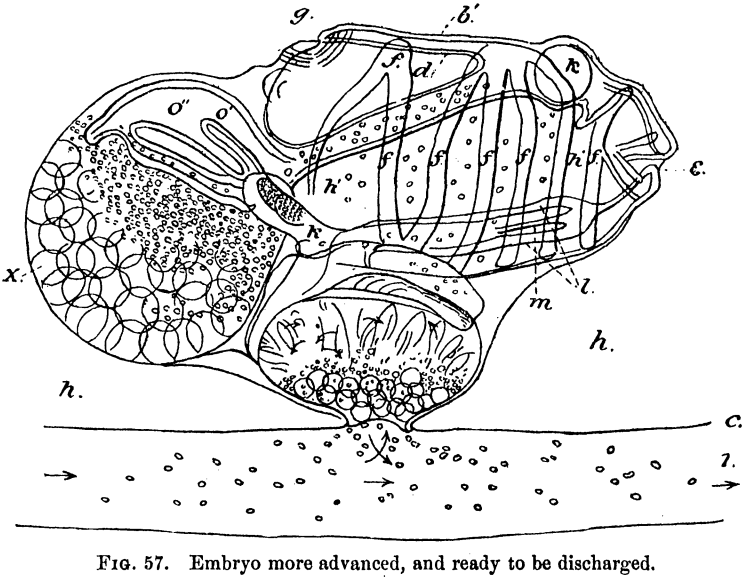


FIG. 57. Embryo more advanced, and ready to be discharged.

placenta, and grows very rapidly and soon assumes the characteristics of the solitary form. In Figure 57 an embryo is figured as it appears when development is very much advanced. It is seen to be attached by a narrow neck to the wall (*c*) of the breathing chamber (*h*) of the nurse. In this figure, 1 represents the blood-channel of the chain-salpa, and the arrows show the direction of the currents into and out of the placenta. The presence of a true placenta in an animal so simple in structure and so far removed from the mammalia is such a remarkable and interesting instance of the independent appearance of similar structures that a short description of it will not be out of place. It is composed of two parts: an inner chamber in direct communication with the blood system of the chain-salpa, and an outer chamber surrounding the inner but entirely shut off from it, and in free communication with the blood system of the fœtus.

The blood globules of the fœtus are much smaller than those of the nurse, and may therefore be distinguished from them without difficulty, and after the heart of the fœtus begins to beat, it is easy to see that there is no direct mingling of the blood of the nurse with that of the fœtus, but simply a very close contact, exactly as is the case in the mammals. The large globules of the nurse can be seen to enter the inner chamber of the placenta, course around it through the intricate channels into which it is divided, and then leave it to return to the general circulation; while the smaller globules of the fœtus may be seen to make their way into and around the outer chamber, and then to return into the general circulation of the fœtus. Since the reversal of the action of the heart of the fœtus does not generally take place at the same time with that of the chain-salpa, the complete independence of the two circulations is very clearly shown when either of them is reversed.

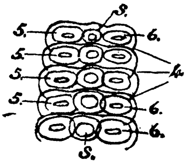
After the embryo has acquired all the organs of the solitary form and has increased many hundred times in size, its attachment by the placenta to the wall of the breathing chamber of the nurse is broken, and the young animal falls into this chamber and lives there for some time, but finally escapes through the posterior opening into the water, and at once begins to form chains by budding, as already described. Figure 45 shows a nearly full-grown chain-salpa, which contains a solitary embryo, (*s*). This is free within the breathing chamber, and is ready to be discharged.

Figures 44 and 45 are drawn to nearly the same scale, Figure 45 being only a little more magnified than Figure 44. Figure 44 represents a solitary Salpa, which contains a chain, *u*, which is ready to be discharged into the water, while Figure 45 represents a chain-salpa, containing an embryo of the solitary form, *s*, which is also ready to be discharged. It will at once be seen, by a comparison of these figures, that although the two forms differ little in size when full grown, the solitary form is many hundred times larger than the chain-salpa at birth. After the embryo escapes from the body of the chain-salpa, the testicle of the latter becomes fully developed, and its spermatic fluid is discharged into the water to gain access to the breathing chambers of younger chain-salpæ and fertilize the eggs carried by these.

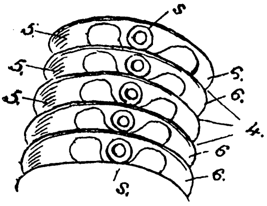
Such is the history of the two forms, as it has been traced by the distinguished naturalists already mentioned, each of whom has added portions of the process which had escaped the notice of the previous observers. Many other embryologists have contributed to our knowledge of the subject, but those mentioned have made Salpa the object of long and exhaustive research, and the summary of their observations may be stated as follows: The egg hatches into an embryo which becomes a solitary Salpa. Each solitary Salpa gives birth to chain-salpæ by a process of budding from the walls of a tube. Each chain-salpa contains a single egg, which undergoes internal impregnation, and forms a solitary embryo, which is nourished by a true placenta. The adult chain-salpa is furnished with a testicle.

From these statements, which are perfectly accurate, the conclusion has been drawn that Salpa presents an instance of alternation of generations. It is almost unnecessary to say here that this term is applied to the reproductive process of those animals among which the egg gives rise to a sexless animal which in time gives origin, by a process of budding, to sexual forms, which in turn reproduce the sexless form by eggs. The hydroids furnish well-known illustrations of this process.

Since in Salpa the eggs as well as the male fluid are found in the animals of the chains, while these are produced asexually as buds from the body of the solitary Salpa, it seems reasonable to conclude that the reproductive process in Salpa is similar to that of the hydroids, the solitary form being the sexless and the chain-salpa the hermaphrodite sexual form; and this view is now generally accepted. I have said that the account which I have given above, and which seems to fully support this conclusion, is strictly accurate; but it is not quite complete. A few of the early stages of development have escaped the notice of all observers, and these few stages put the whole matter in an entirely new light, for they show that the solitary Salpa is the female, and the parent not of the males alone but of the eggs which they carry as well, and therefore of the embryos which these eggs produce. Although the chain-salpa gives birth to the solitary form, it is not its mother, but simply a nurse. It is not even the father of the egg which is fertilized within its body; although, after it has discharged its own embryo it may become the father of the embryos carried by other chain-salpæ. In order to explain this utterly anomalous and apparently contradictory manner of development, it will be necessary to trace a little more minutely the early stages in the formation of the animals which compose the chain. It will be well to call attention, in the first place, to the fact that no female animal or plant we know of has the power to form only a single egg or seed, and it is plain that if there were such an organism, it would gradually become extinct, since each generation could be as numerous as the one before it only when every embryo survived all accidents and reached maturity.



(FIG. 58.)



(FIG. 59.)

Fig. 58. Five Salpæ from a tube, at a very early stage of development.
Fig. 59. The same, still earlier : 4, the constrictions which mark out the animals ; 5, ganglia ; 6, digestive organs ; *s*, ovum.

The fact that the chain-salpa contains only one egg is in itself enough to excite a suspicion that it is not the true female ; but in answer to this argument it might be said, fairly enough, that the whole history of Salpa is a series of anomalies, and that, since one more or less would not make much difference, there is no great difficulty in believing that it differs from all other animals in producing only one egg. It might be urged that indefinite multiplication is provided for by the power of the solitary form to produce large numbers of chains. As we trace back the development of the chain-salpa we soon find much stronger reasons for doubting that this is the parent of the egg which it contains. The sexual products are not usually matured until the animal has reached its adult form, and very few animals reproduce during their embryonic or larval stages; but almost immediately after the chain-salpa is born, and when it is less than a fiftieth of its adult size, its egg is fertilized. Going back to a still earlier period we find that when the organs of the chain-salpa first begin to make their appearance upon the walls of the tube, each one contains a full-grown egg, as shown at *s* in Figure 58. At a still earlier period, when the only indication of the future chain-salpa is the constriction upon the surface of the tube, each space thus marked off contains a single, full-grown egg, which appears to be as fully ripe as at the time of impregnation. Figure 59 shows five of these constrictions at this time, and their eggs (*s*).

At a still earlier stage, before the constrictions appear upon the wall of the tube, this is seen to contain two large club-shaped bodies (Figure 47, *yy*), which under careful examination with high powers are found to contain germinative vesicles; and by patient examination of large numbers of solitary Salpæ at about this period, a few may be found which show that these bodies are made up of rows of eggs and are therefore ovaries, and the solitary Salpa must be regarded as the female, since the chain-salpa cannot be the parent of an egg which exists before the chain-salpa itself is formed.

We must therefore conclude that, instead of an instance of "alternation of generations," we here have simply a remarkable difference in the form and mode of origin of the two sexes, for we must regard the solitary Salpa as the female and the chain-salpa as the male. The life-history of Salpa may then be briefly stated in outline as follows: The solitary Salpa is the female, and produces a chain of males by budding, and discharges a single egg into the body of each of these before birth. These eggs are impregnated while the chain-salpæ are very small and sexually immature, and develop into females which give rise to males by budding. After the fœtus has been discharged from the body of the male the latter attains its full size, becomes sexually mature, and discharges its spermatic fluid into the water to gain access to the eggs carried by other immature chains.

It is worthy of notice that although Chamisso's announcement of the occurrence of alternation of generations among animals is thus seen to have been drawn from the study of animals which do not present an instance of it, this mistake has been of the greatest usefulness, since it has led to our knowledge of the numerous instances of true alternation which now form such a large and important chapter of zoölogical science. The relation in which Salpa stands to the other tunicates shows also that no abrupt line can be drawn between alternation and ordinary sexual reproduction, but that they are different forms of the same process. In a future paper I hope to say a few words upon this subject, and to show how all the strange peculiarities of Salpa receive a simple explanation upon the theory that it is the descendant of an ordinary tunicate which has been modified by natural selection.

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PLAIN, PRAIRIE, AND FOREST.

BY PROF. J. D. WHITNEY.

PART II.

THE more the prairies are studied, the less will one feel disposed to adopt any theory for their origin dependent on climate, and the more will the attention be turned to the question of the character of the soil, the distribution of the geological formations from which this soil has been derived, and the cycle of recent geological events by which it has been distributed and accumulated in its present position. It is evident, however, that in the discussion of a question of this kind full details of the observations made cannot be given ; they would occupy volumes. It is for the observer himself, on carefully analyzing and classifying the results of his examinations, to state the conclusions at which he has arrived ; a catalogue of the localities visited would be of little service to any one else in enabling him to form an independent opinion.

As the result of a great number of observations made over all the prairie States, we find, almost without exception, that absence of forests is connected with extreme fineness of soil, and that this fine material usually occurs in heavy deposits. It seems hardly necessary to enlarge on the characteristics of the so-called "prairie soil." To look at a plow with which the prairie has been broken up ought to be a sufficient indication of this fineness. How often has the writer admired the beautiful polish put upon this common utensil used on the western prairies, and contrasted its appearance with that of the scratched and battered article with which the hills of New England had been belabored. Let us, however, quote a few paragraphs illustrative of the nature of the prairie soil from some of the Geological Survey Reports, beginning with that of Illinois.

" All the part of the county [Boone, Illinois] south of the Kishwaukee may be called a treeless prairie, characterized by